JHR 98: 47–68 (2025)
doi: 10.3897/jhr.98.131191
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

Effects of urbanization and floral diversity on the bee community (Hymenoptera, Apoidea) in an oak forest in a Protected Natural Area of Mexico

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Academic editor: Christopher K. Starr | Received 4 July 2024 | Accepted 15 December 2024 | Published 28 January 2025

https://zoobank.org/7630C6EA-2740-4361-BB40-B539A7E87A5A

Citation: Muñoz-Urias A, Araujo-Alanis L, Huerta-Martínez FM, Jacobo-Pereira C, Razo-León AE (2025) Effects of urbanization and floral diversity on the bee community (Hymenoptera, Apoidea) in an oak forest in a Protected Natural Area of Mexico. Journal of Hymenoptera Research 98: 47–68. https://doi.org/10.3897/jhr.98.131191

Abstract

Understanding the effects of urbanization on bee communities is essential for conservation and management programs for these pollinators. We investigated bee communities in two distinct land-use conditions in Mexico: one within the Bosque el Nixticuil-San Esteban-El Diente Natural Protected Area, which represents a conserved oak forest, and the other in a highly urbanized area in adjacent parks located approximately one kilometer from the conservation area in the Metropolitan Zone of Guadalajara with a population of 5.3 million. The objectives of the study were to 1) record the effects of urbanization on bee communities in terms of species richness, abundance and α and β diversity in an oak forest within a natural protected area and the adjacent urban area, and 2) identify the most susceptible bees and those that benefit from urbanization, and 3) to relate vegetation to bee communities. The results of the rarefaction analysis indicate that the protected natural area exhibited significantly higher richness and diversity than the urbanized area. Beta diversity analysis revealed a low species turnover, accompanied by a high rate of bee loss between conditions. A limited number of species demostrate an increase in abundance within urban areas, mainly *Ceratina* species, *Augochlora smaragdina* and *Centris nitida*. Furthermore, the richness of life history traits of bees was analysed. In all cases, the number of species decreased, with mainly non-eusocial, cavity or wood nesting, and polylectic feeding bees prevailing in the urban area. The richness and abundance of bees is related to the richness of plants, so it was expected to find more species and genera in the natural area. In conclusion, urbanization has a negative impact on the richness and diversity of bee communities, as well as on species composition.

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Keywords
Decline bees, flower resources, pollinators, species richness

Introduction

Despite the crucial role of bees in maintaining the health of wild and agricultural ecosystems, recent reports indicate a decline in wild bee populations (Potts et al. 2010). Habitat loss due to deforestation, intensive insecticide use in cultivated areas, the expansion of urban areas, the introduction of exotic species that can transmit diseases and increase foraging competition with native bees, and the possible effects of climate change are key factors contributing to this decline (Winfree 2010). Habitat loss, particularly due to the expansion of urban areas, is considered the primary long-term cause of bee decline (Goulson et al. 2015).

The causes of the decline in bee richness due to urbanization are diverse (Wensel et al. 2020). For example, Martins et al. (2013) mention the scarcity of preserved native vegetation in these environments. In addition, the temporal dynamics of these resources differ due to factors such as continuous watering of green spaces and the presence of exotic ornamental plants that flower at different times than native plants, causing changes in pollinator population dynamics (Wray and Elle 2015).

Urbanization also reduces the possible nest substrates for bees (Theodorou et al. 2020b). Ground-nesting bees decline in urban areas due to the reduction of suitable nesting surfaces (Geslin et al. 2016), while cavity-nesting bees take advantage of gaps in human constructions (Prendergast et al. 2022).

Bees belong to different guilds that respond differently to urbanization depending on their life histories (Prendergast et al. 2022). Urbanization simplifies the landscape and reduces the richness, diversity and phylogenetic groups of flowering plants (Theodorou et al. 2020a). This affects bees, as they feed on nectar as adults and require pollen and flower oils to feed their larvae. In addition, they need such plant resources as leaves and resins as nest materials (Michener 2000). Generalist (polylectic) bee species predominate in cities, but some specialists (oligolectic) may proliferate due to the introduction of exotic flora and ornamental plants (Theodorou et al. 2020a).

Better understanding the effects of urbanization on bee communities has become a critical objective. Although the results of research are variable (Birdshire et al. 2020), most studies report a negative impact of urbanization on some attributes of bee communities, including species richness, overall abundance and/or diversity (Martins et al. 2013; Cardoso and Gonçalves 2018; Razo-León et al. 2018; Zattara et al. 2021). In contrast, other studies have documented comparable or even higher levels of richness, abundance, and diversity in urban relative to natural areas (Carper 2014; Fortel et al. 2014; Lowe and Foltz-Sweat 2017). It is challenging to determine the conservation status of bees. However, some studies based on historical records

reveal worrying data. For instance, in the United Kingdom and the Netherlands, there has been a generalized decline in the richness and abundance of wild bees and other pollinators (Biesmeijer et al. 2006). According to occurrence data from the Global Biodiversity Information Facility (GBIF) the recorded bee species richness has been continuously decreasing since 1990. Furthermore, comparing records prior to 1990 with records from 2006–2015, a 25% loss of bee species was observed (Zattara et al. 2021).

Most previous studies have compared bee diversity between natural and urban areas but have not considered situations where both areas share the same type of vegetation. Furthermore, this study focuses on a unique configuration, in which a highly urbanized area is located next to a protected natural area, the two sharing many of the same plants. These results have the potential to influence urban management strategies by highlighting the importance of urban environmental factors beyond vegetation type and the availability of floral resources. In order to develop effective conservation programs for bee communities and thus mitigate the potential adverse effects on these pollinators (Dalmazzo 2010), it is essential to compare sites with different levels of urbanization. Accordingly, the objectives of the study were to: 1) document the impact of urbanization on bee communities in terms of richness, overall abundance, life history, α and β diversity, when type vegetation is the same as in adjacent natural areas; 2) identify the most susceptible bees and those that benefit from urbanization; and 3) relate vegetation to bee communities.

Material and methods

Study area

The Bosque el Nixticuil-San Esteban-El Diente Protected Natural Area (BENSEDI), with an area of 1,591 hectares is situated in the municipality of Zapopan, approximately 10 km northeast of the city of Guadalajara, at 20°46'N, 103°24'W. It is within the physiographic region of the Trans-Mexican Volcanic Belt and close to the border of the Sierra Madre Occidental. Its average altitude is 1,550 masl (Fierros-López 2008; Hernández et al. 2009). The types of vegetation present include tropical deciduous forest, oak forest, pine forest, gallery forest, and aquatic vegetation. BENSEDI is adjacent to the Guadalajara Metropolitan Zone, with a population of 5.3 million (IIEG 2020). Consequently, this area is undergoing continuous growth and presents a constant pressure to establish new human settlements (Fig. 1) (Hernández et al. 2009).

The climate of this zone, as defined by Köppen and modified by E. García, is classified as AC (w1-w), a sub-humid temperate climate with summer rainfall. The mean annual precipitation ranges from 600 to 900 mm with highest rainfall in July-September. The mean annual temperature is 22 °C, with a maximum of 30 °C and a minimum of 8 °C. The average number of sunny days is 200 (Ayala 1992).

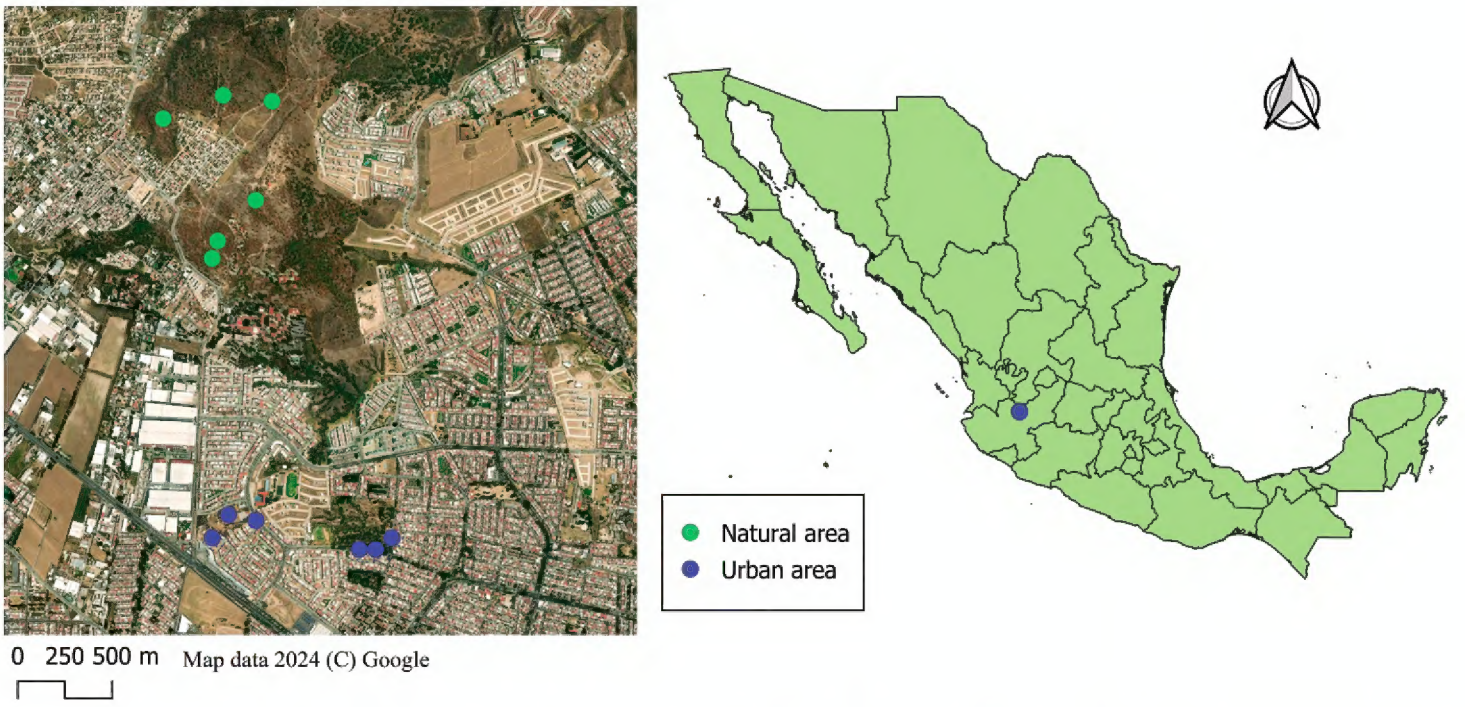

Figure 1. Location of the Bosque el Nixticuil-San Esteban-El Diente Natural Protected Area (NA) and Urban area (UA) sampling sites.

Data collection

A six-month study was conducted from July to December 2022 to assess the diversity of wild bees in the study area. This included the peak of the flowering period in the rainy season, when the emergence of adult bees is higher. The study sites were selected to represent two distinct habitats: 1) A conserved oak forest within the Bosque El Nixticuil-San Esteban-El Diente Protected Natural Area (NA) and a highly urbanized area (UA) with contiguous parks located approximately one kilometer from the BENSEDI. These sites conserve some characteristic trees of the oak forest and some of the herbaceous and secondary vegetation. The study area was urbanized more than 15 years ago.

The bees were collected during four days per month, with particular attention to clear, sunny days. Two sampling days were dedicated to the natural area and two to the urban area. Six plots of 10 × 10 meters were established at random for each condition. The different species of bees and their abundance, as well as the species of plants visited, were recorded during a one-hour period for each plot between 10:00 and 15:00 hours (Wilmer 1983), which is the period of maximum activity for these insects. The bees were captured using an aerial entomological net on flowering plants, in flight, or in their nests. At each site, two individuals were responsible for collecting bees along the established transects.

The specimens were processed in accordance with the standard methodology for bee preservation and identified to the lowest possible taxonomic level using the keys of Michener et al. (1994) and Michener (2000) for the genus level, and mainly the revisions of Ayala (1988), Fierros-López 1998, Hurd and Linsley (1966), LaBerge (1994, 2001), McGinley (1986), Mitchell (1933), Mrida-Rivas (2022), Portman et al. (2022), Roubik and Hanson (2004), Shinn (1967), Snelling (1974, 1990). Individuals that could not be identified to a species were grouped into morphospecies.

Samples of the bee specimens were deposited in the Center for Zoological Studies of the University of Guadalajara (CZUG). Vegetation sampling was carried out within the established plots, where the species of melittophylous plants were recorded and specimens collected for identification.

Data analysis

In order to quantify the species richness (q0) and diversity of bee species, and diversity based on the effective number of common species (q1, exponential of Shannon index) and dominant species (q2, inverse of Gini-Simpson index), we employed rarefaction/extrapolation curves with bee abundances based on samples with equal completeness. Curves were generated using the bootstrap method of Chao and Jost (2012), implemented in R software with the iNEXT package (Hsieh et al. 2016). Furthermore, rarefaction/extrapolation curves with frequencies for plant species visited by bees within the established plots were developed using the same method.

Bee specimens were classified by life history trait information for each bee species according to Michener et al. (1994), Michener (2000), Hoehn et al. (2008) and Moretti et al. (2009).

The bees were classified according to social habit (eusocial or non-eusocial), nesting habit (in soil, pre-existing cavities, or wood), and feeding habit (polylectic or oligolectic; Michener 2000).

Life history trait richness was compared between the natural and urban areas, using Pearson's chi-squared test to assess differences in total non-eusocial, cavity nesting and polylectic bee species. However, in the urban area, some life history traits had only one species with a single specimen, which prevented further statistical analysis. In addition, a binomial proportional analysis was carried out to determine whether the proportions of life-history traits remained constant despite a decline in species richness. This analysis compared the richness of bees with different traits unique to the natural area to those in the urban area.

A generalized linear model (GLM), was employed to assess the bee abundance and native bee abundance (excluding *Apis mellifera*), using the number of individuals per plot and a Pearson's chi-squared test to evaluate differences in total abundances in bee family in relation to natural area and urban area, through the use of R software (R Core Team 2016). Furthermore, the asymmetry index of abundances was estimated for the bee species shared between the two conditions at a 1:1 ratio. This index is standardized between values from -1 to 1, with values close to zero indicating the same abundance for both locations, values close to -1 indicating a higher affinity to urban area, and values close to 1 indicating a higher relationship to natural area based on abundance. This method was modified from that of Blüthgen et al. (2006).

$$\text{Abundance asymmetry} = \frac{\textit{Abundance of sp. in NA} - \textit{Abundance of sp. in UA}}{\textit{Abundance of sp. in UA} + \textit{Abundance of sp. in NA}}$$

The abundance of the most common bee genera (*Apis*, *Centris*, *Ceratina* and *Megachile*) was compared between the natural and urban areas using Pearson's chi-square test. The other genera could not be statistically analyzed due to the low number of recorded specimens (singletons or doubletons).

The β diversity of bees between the two different conditions was analyzed according to the method of Baselga (2010). The Sorensen's dissimilarity index βSor is decomposed into species turnover (βSim) and nesting components (βSne) using the vegan software package R (Oksanen et al. 2013). To relate bee genera to the plant families they visit in relation to the two conditions, non-metric multidimensional scaling (NMDS) using Wisconsin transformation of the abundance and finally we correlated the abundance family of plant with data ordenation using the envfit funtion using R software, and the vegan package (Oksanen et al. 2013). Finally, the relationship between bee abundance and richness were related to plant richness using generalized linear model (GLM) considering that the distribution of the data is quasi-Poisson, this was conducted using base R software.

Results

Sampling efficiency and comparison of specific richness

A total of 2,322 specimens were recorded, representing 95 species (Table 1, Appendix 1).

The interpolation/extrapolation curves demonstrate a notable disparity in species richness between the protected natural area and the urban area. A sampling efficiency of 70% was observed for the natural area, with an estimated 134 species, and 87% for the urban area, with an estimated 18 species of bees (Fig. 3). In the natural area, the genera that exhibited the highest richness were *Megachile* (13 species), *Lasioglossum* (11 species), *Andrena*, *Augochlora*, and *Ceratina* with 5 species respectively. In contrast, the genera with the highest richness in the urban area are: The genera *Ceratina*, *Centris*, and *Megachile* are represented by three species each.

Bee richness in all life history traits decreased in the urban area relative to the natural area. In the natural area three species are eusocial: *Apis mellifera*, *Augochlorella neglectula* and *Halictus ligatus*, while the introduced *A. mellifera* is the only eusocial

Table 1. Richness and abundance of bees recorded in both conditions, natural area (NA) and the urban area (UA).

Family	Richness in NA	Richness in UA	Abundance in NA	Abundance in UA
Apidae	34	11	1,245	747
Halictidae	20	2	60	13
Megachilidae	21	2	128	8
Colletidae	4	0	18	0
Andrenidae	15	0	103	0
Total	**94**	**15**	**1,554**	**768**

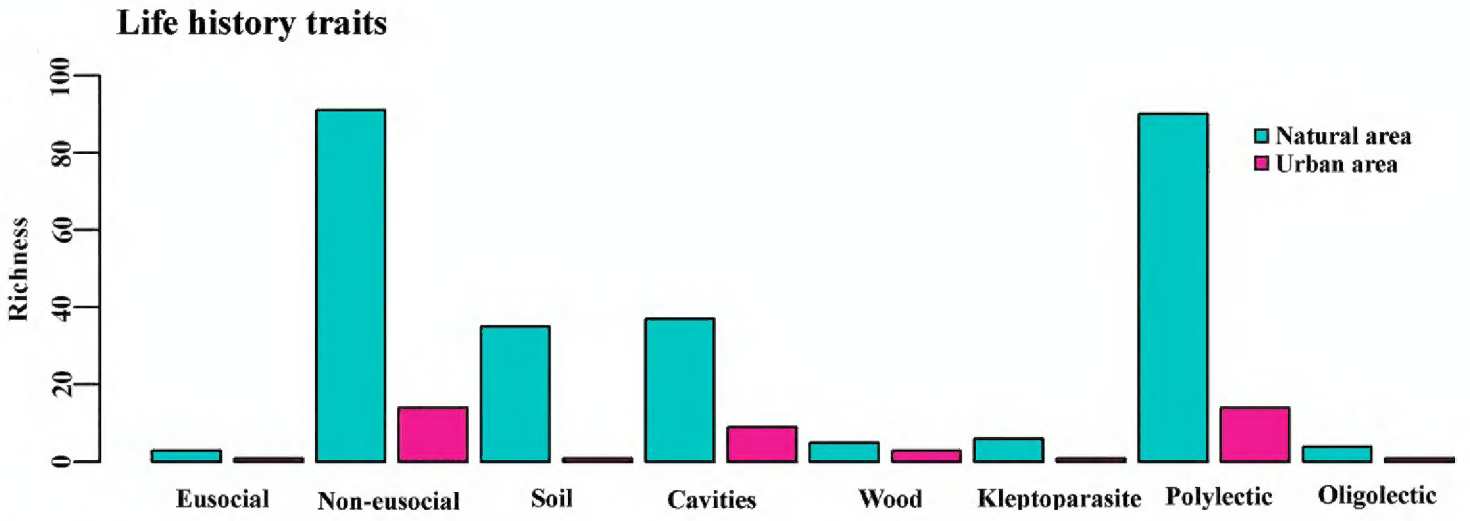

Figure 2. Bee richness of different life history traits between natural area (NA) and urban area (UA).

species in the urban area. No significant differences were found in the proportions of eusocial bees ($p = 0.96$) between the two areas. A total of 91 non-eusocial species (solitary, subsocial, parasocial or semisocial) were recorded in the natural area, 14 in the urban area. Pearson's chi-squared test showed significant differences in the richness of these species between the two areas ($\chi^2 = 56.4$, $p < 0.05$) (Fig. 2). Despite the decrease in richness, the proportions of non-eusocial bee species showed no significant difference ($p = 0.97$) between the two urban areas.

In the natural area, 35 species nest in the soil, 37 species in cavities, five species in wood, and six are kleptoparasites (*Coelioxys aztecus*, *Coelioxys* sp.1, *Mesocheira bicolor*, *Triepeolus* sp. 1, *Triepeolus* sp. 2 and *Triepeolus* sp. 3). In contrast, in the urban area one species nests in soil, nine species in cavities, three species in wood, and one is kleptoparasitic (*Mesocheira bicolor*). Proportion analysis showed significant differences only in soil-nesting bees between the two areas ($\chi^2 = 5.5$, $p < 0.01$), with a proportion of 0.42 in the natural area and 0.06 in the urban area.

In terms of feeding habits, 90 polylectic species and four oligolectic species were recorded in the natural area. Of the latter species' food plants, *Melitoma marginella* and *M. segmentaria* belong to the family Convolvulaceae, while *Peponapis azteca* and *P. utahensis* are in the Cucurbitaceae. In the urban area, 14 polylectic species and only one oligolectic species (on *M. marginella*) were identified (Fig. 2). Pearson's chi-squared test showed a significant decrease in the richness of polylectic bees in the urban area ($\chi^2 = 55.5$, $p < 0.05$). However, the proportions analysis showed no significant differences (in the proportions of polylectic bees between the natural area (0.96) and the urban area (0.94). Furthermore, no significant differences were observed in the proportions between the natural and urban areas among oligolectic bees.

Abundance

Overall, a 49% reduction in the abundance of bees was observed in the urban area, relative to the natural area ($t = 2.13$, $p = 0.039$). The total number of native bees (excluding *Apis mellifera*) observed in the natural area was 571, in comparison to 171 in

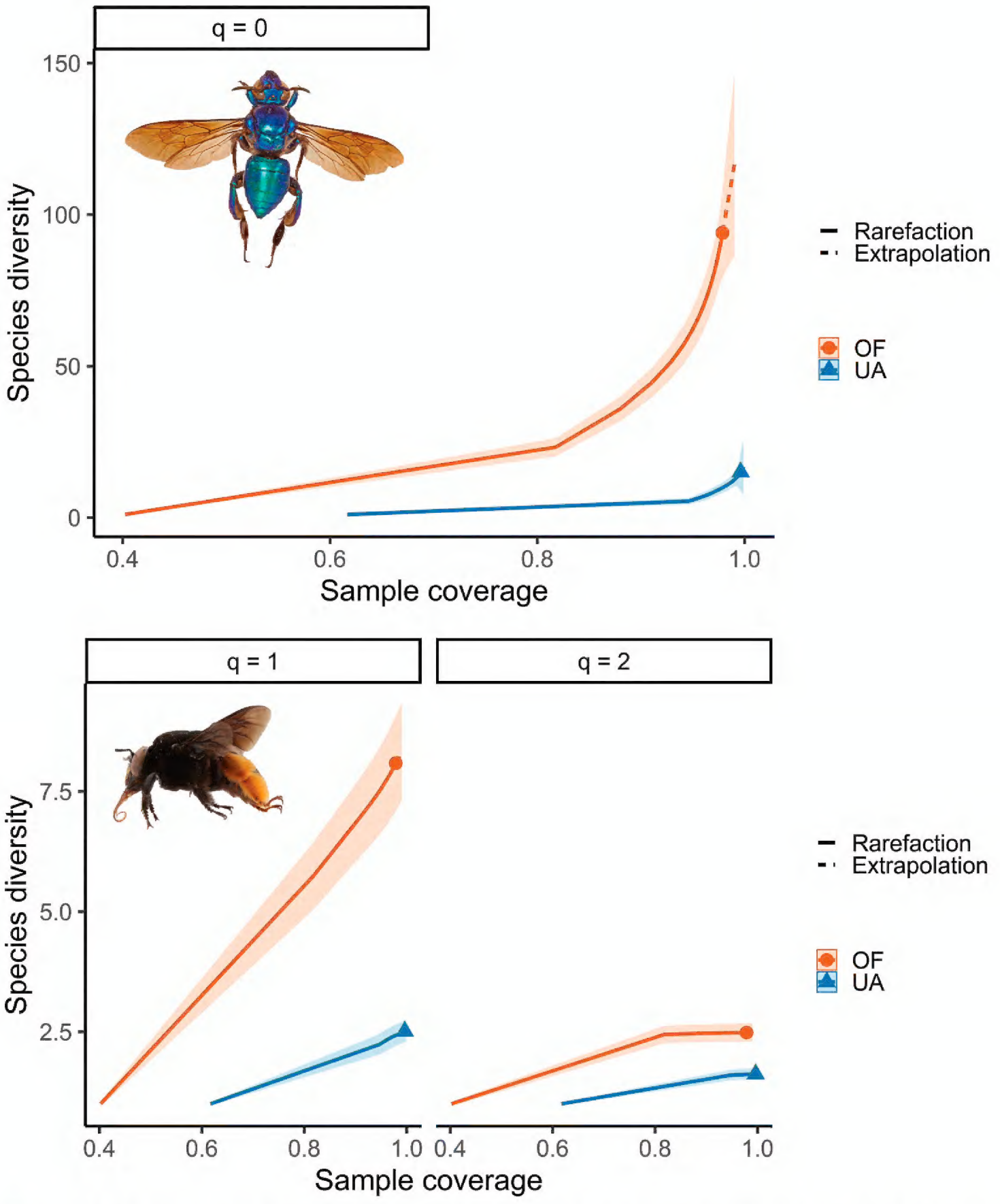

Figure 3. Abundance-based rarefaction (solid line) and extrapolation (dashed line) plots with 95% confidence intervals (shaded areas) comparing: richness (q0), common species (q1) and dominant species (q2) on community bees between the conserved oak forest (NA) and Urban Area (UA).

the urban area. This indicated a notable decline ($t = 3.73$, $p < 0.05$) in the abundance of native bees by 70% in the urban area. Between the two conditions the number of specimens recorded per family presents a significant decrease in Apidae by 40% ($\chi^2 = 124.5$, $p < 0.05$), Halictidae by 80% ($\chi^2 = 30.2$, $p < 0.05$), Megachilidae by 93.7% ($\chi^2 = 105.9$, $p < 0.05$), while Colletidae and Andrenidae were absent from the UA (Table 1).

The most abundant bees in the natural area were *Apis mellifera*, *Melitoma marginella*, *Melissodes tepaneca*, *Centris nitida* and *Andrena* sp. 4, and in the UA *Apis mellifera*, *C. nitida* and *Ceratina* sp. 4. Of the 15 bee species present in the UA, nine showed greater abundance relative to the natural area, especially species of *Ceratina*, *Augochlora* and *Centris*, while the other six showed a reduced abundance (Table 2).

The most abundant genera in both areas were *Ceratina* and *Centris*. In contrast, the abundance of *Apis* and *Megachile* was significantly higher in the natural area ($p < 0.05$).

Diversity α and β

Diversity based on common species (q1) shows a significant decrease as the confidence intervals do not overlap between the different conditions, going from 8.5 species common in the natural area to 2.5 species in the UA. Similarly, diversity based on dominant species (q2) is higher in NA with 2.5 species to 1.6 species in UA (Fig. 3).

Regarding beta diversity, 14 bee species are common in both conditions (ubiquitous), while 80 species are exclusive to the Oak Forest, and only one species is unique to the Urban Area (Fig. 4). The dissimilarity between the different conditions is high due to the fact that few bee species are shared between the two areas. Since βSor presents a value of 0.72, beta diversity was mostly attributed to the nesting of the species assemblage (βSne = 0.72) due to the loss of species in the urban area compared to the natural area. Species turnover is very low (βSim = 0.0) because the species present in the urban area are those that tolerate habitat disturbance and can remain in these sites.

Table 2. Bee species, number of specimens, and asymmetry of abundance. Values close to -1 indicate higher abundance in urban area (UA), while those close to 1 indicate a higher abundance in natural area (NA).

Species	Abundance in NA	Abundance in UA	Asymmetry of abundance
Ceratina sp. 3	0	7	-1
Ceratina sp. 2	1	7	-0.75
Ceratina sp. 4	9	52	-0.70
Augochlora smaragdina	3	9	-0.50
Centris nitida	26	68	-0.44
Centris varia	1	2	-0.33
Centris atripes	6	10	-0.25
Ashmeadiella sp. 1	2	3	-0.20
Lasioglossum (*D.*) sp. 1	3	4	-0.14
Apis mellifera	978	597	0.24
Mesocheira bicolor	5	2	0.42
Megachile sp. 2	23	1	0.71
Thygater montezuma	17	1	0.89
Megachile flavihirsuta	24	4	0.91
Melitoma marginella	65	1	0.97

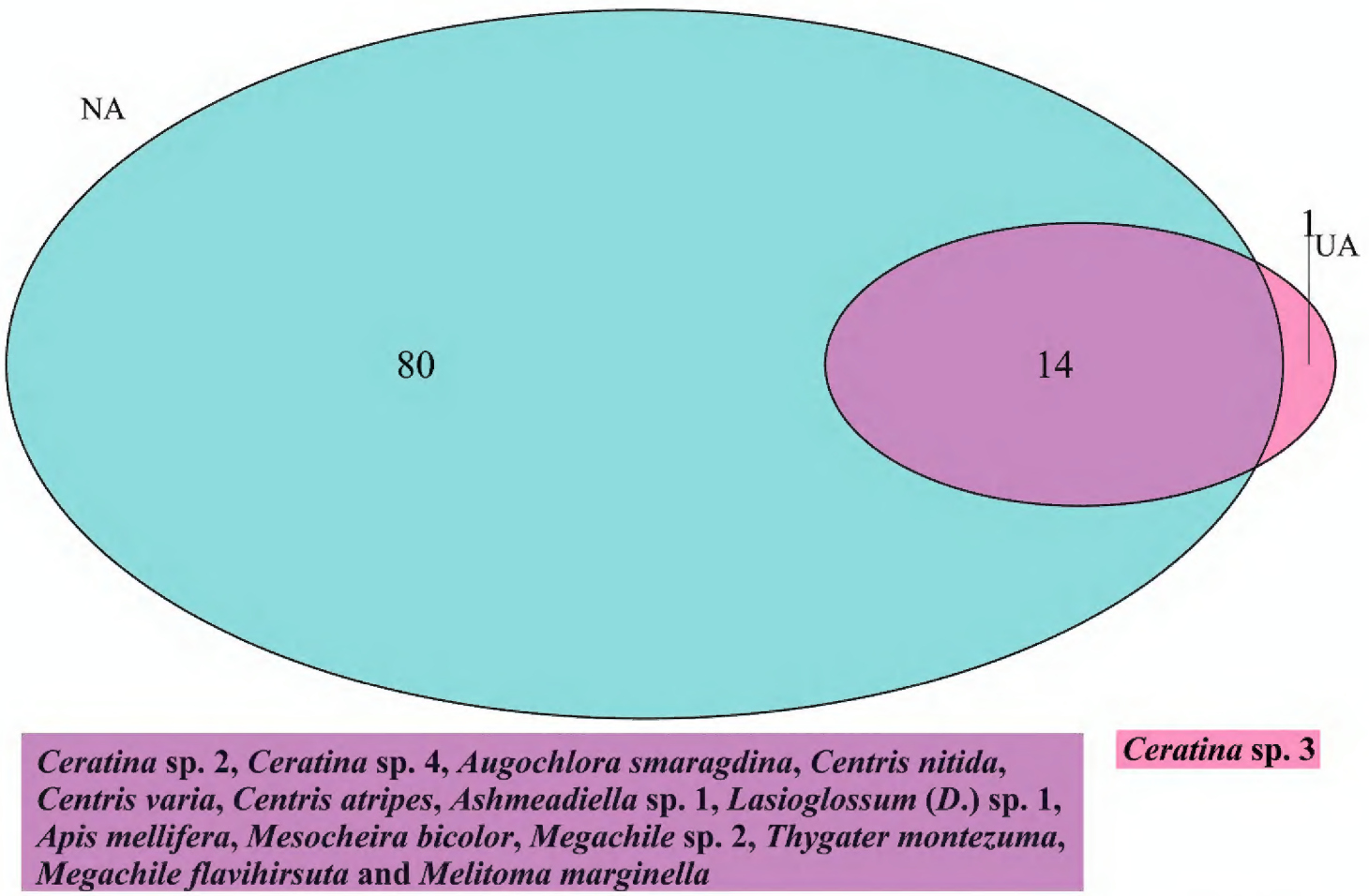
NA
80
14
1
UA
Ceratina sp. 2, *Ceratina* sp. 4, *Augochlora smaragdina*, *Centris nitida*, *Centris varia*, *Centris atripes*, *Ashmeadiella* sp. 1, *Lasioglossum* (*D.*) sp. 1, *Apis mellifera*, *Mesocheira bicolor*, *Megachile* sp. 2, *Thygater montezuma*, *Megachile flavihirsuta* and *Melitoma marginella*
Ceratina sp. 3

Figure 4. Venn diagram of species recorded in the natural area (NA, blue), in the urban area (AU, pink), and species shared between the two areas (purple).

Plants visited by bees

In the natural area we recorded bee visits to 40 plant species from 14 plant families, most prominently Asteraceae (13 bee species), Fabaceae (9 species) and Lamiaceae (4 species). The plants most visited by bees were *Cosmos sulphureus* (37 bee species), *Bidens odorata* (22 species), *Cosmos bippinatus* (19 species) and *Dalea versicolor* (17 species). The bees that visited the greatest variety of plants were *Apis mellifera* (17 spp.), *Melissodes tepaneca* (10 species), *Megachile albitarsis* (9 species) and *Exomalopsis moesta* (8 species).

On the other hand, in the urban area only nine plant species from six families were visited by bees, including Asteraceae (3 bee species) and Convolvulaceae (2 species).

According to the frequency-based rarefaction curves, the natural area presented a significantly higher richness (q0) of melittophylous plant species, with an estimate of up to 77 species, while in the UA a richness of 10 species of plants visited by bees is estimated, so that urbanization drastically reduces the floral resources used by bees, The diversity of melittophylous plants is also strongly reduced from 37 estimated common species (q1) to only 10, and there was a significant reduction due to urbanization in the dominant plant species (q2), where in the natural area 24 plant species were estimated in relation to the UA, with only eight dominant species estimated for this higly human-modified area (Fig. 5). It was observed that bee abundance is related to plant richness ($d^2 = 0.4224$), this same trend was observed between bee species richness with plant richness ($d^2 = 0.6611$) (Fig. 6).

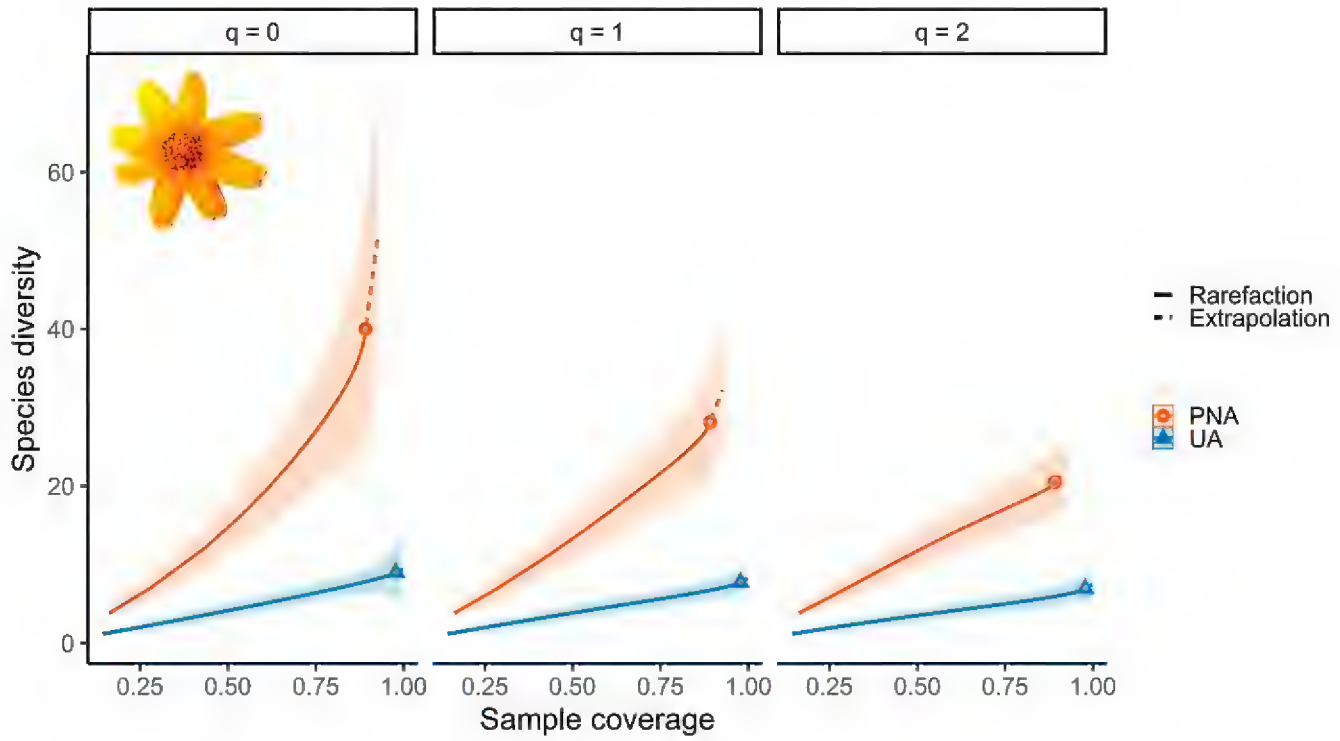

Figure 5. Frequency-based rarefaction (solid line) and extrapolation (dashed line) plots with 95% confidence intervals (shaded areas) comparing: Richness (q0), common species (q1) and dominant species (q2) on community of plants visited by bees between conserved oak forest (NA) and Urban Area (UA).

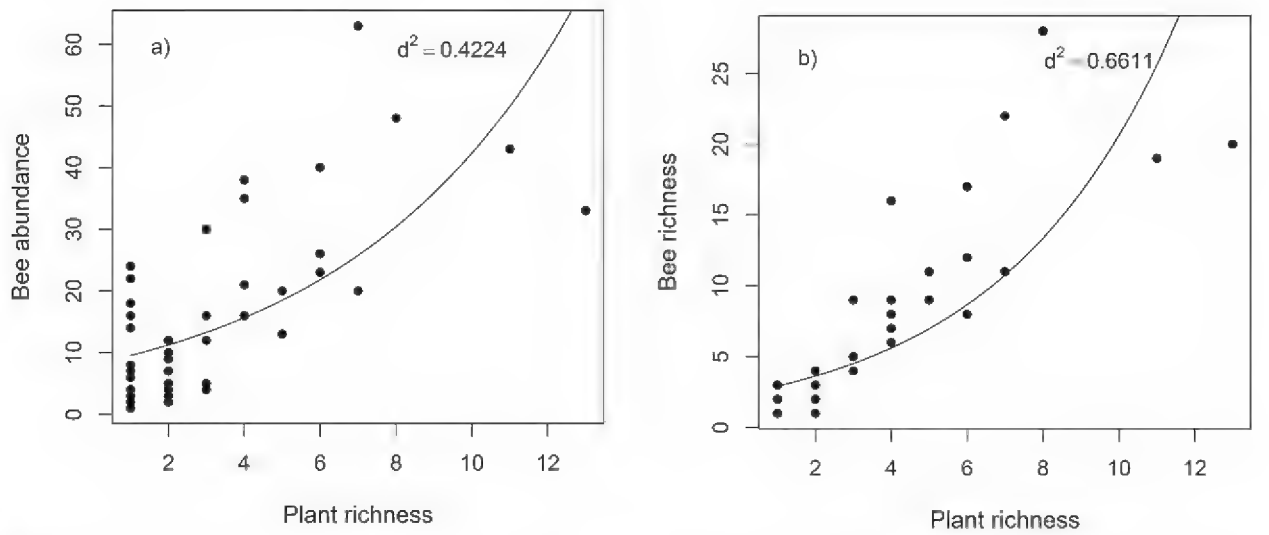

Figure 6. Correlation between **a** plant richness and bee abundance **b** plant richness and bee species number across the sampled areas.

The NMDS analysis showed a low stress value (0.09), the sites sampled in the urban area were located to the right of the graph, while the sites in the natural area were located to the left, both conditions showing a disjunct distribution ($r^2 = 0.65$, $p = 0.004$). In addition, it was observed that the genera *Apis*, *Ashmeadiella*, *Centris* and *Ceratina* were associated with the urban area, while *Augochlora* and *Mesocheira* are in the middle of the graph, as they are found in both areas. The remaining genera were associated with the natural area. The envfit function showed that the number of bee interactions with the families Commelinaceae ($r^2 = 0.42$, $p = 0.08$), Convulvulaceae ($r^2 = 0.65$, $p = 0.008$) and the richness of the plant families are correlated ($r^2 = 0.78$, $p = 0.001$) with the NMDS values corresponding to the natural area, while the number of interactions with the family Cyperaceae ($r^2 = 0.73$, $p = 0.09$) is correlated with the NMDS values of the urban area (Fig. 7).

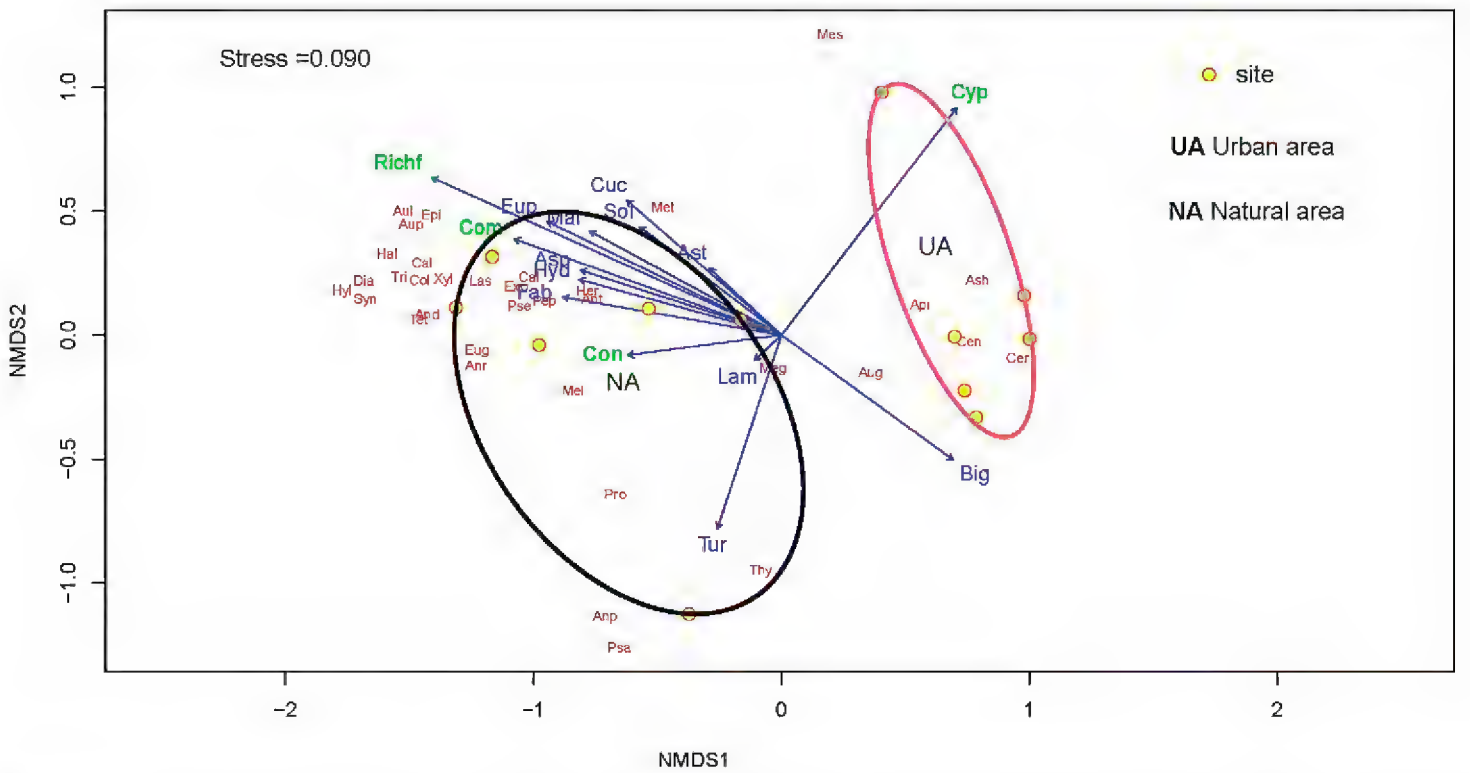

Figure 7. Ordination diagram derived from NMDS showing bee genera in relation to plant families in the natural area (NA) and urban area (UA). Bee genera are represented by acronyms in red labels, while vectors are generated based on the values of the plant family richness variables. Acronyms in blue labels are not significant, while those in green labels are significant ($p < 0.1$). A list of abbreviations can be found in Appendix 2.

Discussion

The response of bees to urbanization depends on intrinsic species traits (Birdshire et al. 2020) as well as local habitat characteristics. We recorded an 84% reduction in bee species richness in the urban relative to the natural area. That is, 15 species in the urban area, 94 in the natural area. These data are consistent with those from other studies; 44 bee species have been recorded from urban metropolitan Guadalajara (Fierros-López 2004), while in the natural areas surrounding the city totals vary between 81 and 94 bee (Fierros-López 1998; Serrano et al. 2015; Razo-León 2024).

In addition, the abundance of bees decreased by 50%, and considering only native bees, a 70% decrease in the number of bees was observed. Short-tongued bee families, such as Andrenidae and Colletidae, are disappearing from urban areas, with Halictidae also showing a significant decline. These bees, often specialized in foraging on flowers with reduced corollas (Fortel et al. 2014). These bees are particularly vulnerable to any reduction in vegetation cover (Banaszak-Cibicka and Żmihorski 2012; Razo-León et al. 2018).

Megachilidae also show a marked decline in both richness and abundance in urban environments. This may be due to their nesting, which requires specific cavities and materials (O´Toole and Raw 1999; Michener 2000). It is likely that these resources are much reduced in urban areas.

In the natural area eusocial bees, mainly represented by *A. mellifera*, account for about 63% of the total abundance recorded. In contrast, in the urban area, *A. mellifera* still accounts for 77% of the individuals observed despite the overall decline in bee

abundance. Similar results were observed by Guimarães and Gaglianone (2021), who reported that in urban areas, eusocial bees represented 82% of the observations. The decrease in richness and abundance of other bee species causes *A. mellifera* to become a more dominant species, as also observed by Cardoso and Gonçalves (2018). It seems that eusocial bees are more resilient to urbanization than other bee groups (Graf et al. 2022). This may be attributed to the slight differences in the proportions of eusocial bees between the two areas. However, non-eusocial bees exhibited a notable decline in richness, potentially since numerous species present in the natural area and absent in the urban area possess narrower niches, making it difficult for them to maintain populations in these environments.

The findings revealed that soil-nesting bees exhibited a pronounced sensitivity to urbanization, manifested in a pronounced reduction in their richness and proportion in the urban area relative to the natural area. This is consistent with other studies showing that these bees are underrepresented in urban area, since that they require bare soil in order to establish their nest (Geslin et al. 2016; Prendergast et al. 2022; Theodorou et al. 2022a). These include members of the families Andrenidae, Colletidae and some Halictidae, which may contribute to their decline or scarcity in urban environments (Cane 2006). Conversely, a reduction in the richness, but not in the proportion, of cavity-nesting bees is observed when comparing the two areas. The present study and other authors (Cane 2006; Theodorou et al. 2022b) show that cavity-nesting bees are more prevalent in urban areas, as they can exploit nesting sites associated with building. In contrast, no significant differences in richness were observed among the different areas for wood-nesting bees.

Kleptoparasitic bees, which lay eggs in the nests of other bees (Michener 2000), have shown a reduction in richness and abundance due to their vulnerability to habitat disturbance (Job and Olakkengill 2016). In the urban area, only one species, *Mesocheira bicolor*, was recorded, with a single individual parasitizing bees of the genus *Centris*. A decline in oligolectic bees was observed in the urban area. The absence of Cucurbitaceae explains the lack of *Peponapis* bees, while the scarcity of water and suitable nesting conditions, such as vertical clay walls, likely caused the near absence of *Melitoma marginella* despite the presence of Convolvulaceae in the urban area (Dalmazzo 2010).

Fifty bee species were recorded in the urban zone, of which nine showed a higher abundance in this environment. Some species within two genera stand out: *Ceratina* and *Centris*, which seem to show a preference for urban area; both are polylectic, visiting a wide variety of plants, allowing them to do well in urban areas (Razo-León et al. 2018). *Ceratina* nests in small hollow stems (Michener 2000), which can be found in urban parks due to the maintenance of plant pruning. *Centris* nest in pre-existing cavities, allowing them to use holes in buildings as nest sites. And *Centris nitida*, which is the most abundant native bee in the UA, has been recorded as a common species in other urban areas, where it can be found in gardens and parks (Pemberton and Liu 2008).

Hung et al. (2017) points out that urbanization exerts significant effects on bee beta diversity, which can serve as an index of the impact of anthropogenic disturbances

on the communities of these pollinators. It has been reported that natural habitats harbor higher bee diversity and that most species show preference for forested habitats and few species prefer disturbed habitats.

The low similarity between urban and natural areas is mainly explained by loss of species (βSne), rather than their replacement. Pereira et al. (2021) found that differences in bee β diversity in urbanized sites over time were mainly explained by the loss of bee species with specific foraging and nesting habits.

Species turnover (βSim) was low, with only one exclusive bee species found in the urban area and 14 species found in both conditions. This can be explained by the presence of generalist and opportunistic species that can thrive in urbanized areas, along with introduced bee species such as *A. mellifera* (Collado et al. 2019).

A significant reduction in the richness (q0) and diversity (q1, q2) of plant species visited by bees was observed in the urban area. There was also a positive correlation between the richness of melittophile plants and the number of bee species and their abundance. Flowers as a food resource, in combination with abiotic factors, give rise to two different bee communities in natural and urban areas. Vegetation, including its abundance, herbaceous cover, floral trait diversity, and canopy cover, has been found to directly influence bee communities in terms of their abundance, composition, and diversity (Ayers and Rehan 2021).

Floral resources are among the most important and consistent predictors of bee diversity and pollinator population size (Gruver and CaraDonna 2021). As can be observed, most bees are present in the natural area, as most plant families are also associated with this area. Several plant families, including Commelinaceae, are exclusive to this area, while others, such as Convolvulaceae, which are shared, exhibit greater diversity and are visited by a greater number of bees in the natural area. In contrast, the urban area exhibits a notable association with the Cyperaceae. It has been documented that the implementation of an intensive management strategy for urban green areas, encompassing regular pruning and irrigation, has been observed to facilitate the proliferation of grass species (Aronson et al. 2017). Additionally, the Bignoniaceae, represented by the *Tecoma stans*, is tolerated in this area as an ornamental tree throughout the city.

Our study reveals that urbanization leads to a drastic reduction in the richness, abundance and diversity of bee communities. Therefore, it is critical to protect areas of native vegetation, as they act as reservoirs of pollinator species essential for reproduction and succession in forest ecosystems and may harbor bee species of great economic importance for crops (Ayers and Rehan 2021). For example, bees of the genus *Peponapis* are highly efficient pollinators of squash, while megachilids and halictids contribute to the production of crops such as various Asteraceae, Rosaceae, and legumes such as beans and chili. Likewise, bees of the family Colletidae can be important pollinators of chayote (Vergara et al. 2023).

It is essential to strengthen the conservation of the Bosque el Nixticuil-San Esteban-El Diente Protected Natural Area, despite the pressures to change its land use. In addition, it is essential to promote urban planning that considers the creation of large

green areas with abundant floral richness and coverage, to mitigate the negative impacts of urbanization on bee communities (Guimarães and Gaglianone 2021).

Finally, it is recommended to create open areas in the study zone where herbaceous patches can develop, including different species of native plants, secondary and ornamental vegetation, but also favoring the presence of different plant families. to promote an increase in bee diversity and prevent the elimination herbaceous plants as part of the maintenance of the urban park, as well as to increase the density of trees. Another proposal to mitigate the effects of urbanization on bee communities could be the creation of bare ground areas with different substrates and degrees of slope hospitable to soil-nesting bees.

However, urban landscapes may be conducive to the conservation of some taxa, particularly solitary, cavity-nesting bees or those favored by anthropized environments, such as the family Halictidae (Razo-León et al. 2018; Ayers and Rehan 2021).

Acknowledgments

We thank the reviewers (Makaylee Crone and Christopher K. Starr) for critical comment on an earlier version, CONAHCYT and the University of Guadalajara for institutional support, the Municipality of Zapopan for research support, and the students Kenia Isabel Francisco Castro, Leonardo Daniel Meléndez Barajas and Linda Elizabeth Vargas Gutiérrez for their participation in the project, and Gaven Peggs for help with the language.

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Appendix 1

Table A1. Number of individuals according to species recorded in different land use conditions: Protected Natural Area (PNA) and Urban Area (UA). Life history traits: Social habit (Soc): Eusocial (E) or Non-eusocial (NE). Nesting habit (Nst): Soil (S), Cavities (C), Wood (W), and Kleptoparasitic (K). and Feeding habit (Fh): Polylectic (P), Oligolectic (O).

Species of bees	NA	UA	Soc	Nst	Fh
Andrena sp. 1	10	0	NE	S	P
Andrena sp. 2	1	0	NE	S	P
Andrena sp. 3	7	0	NE	S	P
Andrena sp. 4	25	0	NE	S	P
Andrena sp. 5	1	0	NE	S	P
Anthidium maculifrons Smith, 1854	11	0	NE	C	P
Anthophora capistrata Cresson, 1878	2	0	NE	S	P
Anthophora sp. 1	1	0	NE	S	P
Anthophora squammulosa Dours, 1870	8	0	NE	S	P
Anthophorula sp.1	1	0	NE	S	P
Apis mellifera Linnaeus, 1758	978	587	E	C	P
Ashmeadiella sp.1	2	3	NE	C	P
Augochlora aurifera Cockerell, 1897	10	0	NE	C	P
Augochlora quiriguensis Cockerell, 1913	6	0	NE	C	P
Augochlora sidaefoliae Cockerell, 1913	2	0	NE	C	P
Augochlora smaragdina Friese, 1917	3	9	NE	C	P
Augochlora sp. 1	1	0	NE	C	P
Augochlorella neglectula (Cockerell, 1897)	2	0	E	S	P
Augochloropsis metallica (Fabricius, 1793)	1	0	NE	C	P
Calliopsis hondurasica Cockerell, 1897	10	0	NE	S	P
Calliopsis sp. 1	1	0	NE	S	P
Calliopsis sp. 2	1	0	NE	S	P
Centris atripes Mocsáry, 1899	6	10	NE	C	P
Centris nitida Smith, 1874	26	68	NE	C	P
Centris varia (Erichson, 1848)	1	2	NE	C	P
Centris sericea Friese 1899	3	0	NE	C	P
Ceratina capitosa Smith, 1879	1	0	NE	W	P
Ceratina sp. 1	1	0	NE	W	P
Ceratina sp. 2	1	7	NE	W	P
Ceratina sp. 3	0	7	NE	W	P
Ceratina sp. 4	9	52	NE	W	P
Coelioxys aztecus Cresson, 1878	1	0	NE	K	P
Coelioxys sp. 1	1	0	NE	K	P
Colletes sp. 1	11	0	NE	S	P
Colletes sp. 2	3	0	NE	S	P
Colletes sp. 3	3	0	NE	S	P
Dianthidium sp. 1	1	0	NE	C	P
Epicharis elegans Smith, 1861	2	0	NE	S	P
Euglossa viridissima Friese, 1899	2	0	NE	C	P
Exomalopsis arida Cockerell, 1929	7	0	NE	S	P
Exomalopsis moesta Timberlake, 1890	13	0	NE	S	P
Halictus ligatus Say, 1837	2	0	E	S	P
Heriades sp. 1	4	0	NE	C	P
Heriades sp. 2	3	0	NE	C	P

Species of bees	NA	UA	Soc	Nst	Fh
Hylaeus sp. 1	1	0	NE	S	P
Hypanthidium mexicanum (Cresson, 1878)	1	0	NE	C	P
Lasioglossum acarophyllum McGinley, 1986	2	0	NE	S	P
Lasioglossum desertum Smith, 1879	1	0	NE	S	P
Lasioglossum (*Dialictus*) sp. 1	3	4	NE	C	P
Lasioglossum (*Dialictus*) sp. 2	1	0	NE	C	P
Lasioglossum (*Dialictus*) sp. 3	1	0	NE	C	P
Lasioglossum (*Dialictus*) sp. 4	1	0	NE	C	P
Lasioglossum (*Dialictus*) sp. 5	2	0	NE	C	P
Lasioglossum (*Dialictus*) sp. 6	10	0	NE	C	P
Lasioglossum (*Dialictus*) sp. 7	1	0	NE	C	P
Lasioglossum (*Hemialictus*) sp. 1	1	0	NE	C	P
Lasioglossum (*Hemialictus*) sp. 2	2	0	NE	C	P
Megachile albitarsis Cresson, 1872	17	0	NE	C	P
Megachile exilis Cresson, 1878	12	0	NE	C	P
Megachile flavihirsuta Mitchell, 1939	24	4	NE	C	P
Megachile parallela Smith, 1853	9	0	NE	C	P
Megachile petulans Cresson, 1878	5	0	NE	C	P
Megachile reflexa (Snell, 1990)	2	0	NE	C	P
Megachile sp. 1	4	0	NE	C	P
Megachile sp. 2	2	1	NE	C	P
Megachile sp. 3	2	0	NE	C	P
Megachile sp. 4	1	0	NE	C	P
Megachile sp. 5	1	0	NE	C	P
Megachile sp. 6	1	0	NE	C	P
Megachile sp. 7	2	0	NE	C	P
Megachile zapoteca Cresson, 1872	5	0	NE	C	P
Melissodes communis Cresson, 1878	1	0	NE	S	P
Melissodes sp. 1	21	0	NE	S	P
Melissodes tepaneca Cresson, 187	30	0	NE	S	P
Melitoma marginella (Cresson, 1872)	65	1	NE	S	O
Melitoma segmentaria	4	0	NE	S	O
Mesocheira bicolor (Fabricius, 1804)	5	2	NE	K	P
Peponapis azteca (Hurd & Linsley, 1966)	11	0	NE	S	O
Peponapis utahensis (Cockerell, 1905)	5	0	NE	S	O
Protandrena sp. 1	18	0	NE	S	P
Protandrena sp. 2	11	0	NE	S	P
Protandrena sp. 3	1	0	NE	S	P
Pseudaugochlora graminea (Fabricius, 1804)	5	0	NE	C	P
Pseudopanurgus sp. 1	5	0	NE	S	P
Pseudopanurgus sp. 2	4	0	NE	S	P
Pseudopanurgus sp. 3	7	0	NE	S	P
Pseudopanurgus sp. 4	1	0	NE	S	P
Syntrichalonia fuliginea LaBerge, 1994	1	0	NE	C	P
Tetraloniella balluca LaBerge, 2001	10	0	NE	C	P
Tetraloniella donata (Cresson, 1878)	4	0	NE	C	P
Thygater montezuma (Cresson, 1878)	17	1	NE	C	P
Triepeolus sp. 1	1	0	NE	K	P
Triepeolus sp. 2	1	0	NE	K	P
Triepeolus sp. 3	1	0	NE	K	P
Xylocopa mexicanorum Cockerell, 1912	5	0	NE	W	P
Total	**1554**	**768**			

Appendix 2

Table A2. Names and acronyms of bee genera and plant families at sampling sites for NMDS ordination.

Bee genus	Acronym	Plant family	Acronym
Andrena	And	Asparagaceae	Asp
Anthidium	Ant	Asteraceae	Ast
Anthophora	Anp	Bignoniaceae	Big
Anthophorula	Anr	Commelinaceae	Com
Apis	Api	Convolvulaceae	Con
Ashmeadiella	Ash	Cruciferaceae	Cru
Augochlora	Aug	Cucurbitaceae	Cuc
Augochlorella	Aul	Cyperaceae	Cyp
Augochloropsis	Aup	Euphorbiaceae	Eup
Calliopsis	Cal	Fabaceae	Fab
Centris	Cen	Hydroleaceae	Hyd
Ceratina	Cer	Lamiaceae	Lam
Coelioxys	Coe	Malpighiaceae	Mal
Colletes	Col	Solanaceae	Sol
Dianthidium	Dia	Turneraceae	Tur
Epicharis	Epi		
Euglossa	Eug		
Exomalopsis	Exo		
Halictus	Hal		
Heriades	Her		
Hylaeus	Hyl		
Hypanthidium	Hyp		
Lasioglossum	Las		
Megachile	Meg		
Melissodes	Mel		
Melitoma	Met		
Mesocheira	Mes		
Peponapis	Pep		
Protandrena	Pro		
Pseudoaugochlora	Psa		
Pseudopanurgus	Pse		
Syntricalonia	Syn		
Tetraloniella	Tet		
Thygater	Thy		
Triepeolus	Tri		
Xylocopa	Xyl		